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Eocene Balanidae of Florida, Including a New Genus and Species with a Unique Plan of "Turtle-Barnacle" Organization¹

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INTRODUCTION

Eocene balanomorph barnacles are invariably of interest owing to their relative rarity, but of far greater significance is the evolutionary and phylogenetic information that they may provide. Recently, a brief review of the worldwide stratigraphic and zoogeographic distribution of Eocene Balaninae, including the description of a new species from the late Eocene of Georgia, was presented (Ross, 1965c). The present study is a continuation of work on the fossil Thoracica of the Atlantic Coastal Plain and records three balanomorphs from the Eocene sediments of Florida. In addition, a list of species occurring in the Tertiary and Pleistocene of Florida is provided.

Two of the species discussed herein, *Kathplameria georgiana* Ross and *Balanus* sp. (aff. *B. unguiformis* Sowerby), were collected from the Inglis Limestone. The Inglis is overlain by, and in part interfingers with, the Williston Limestone. Both these stratigraphic units are included in the Ocala Group of late Eocene age (Jackson).

¹ The introductory discussion, systematic descriptions, and the appended list of Florida fossil barnacles were prepared by Ross; the discussion of the ontogeny and phylogeny of the new form described herein was prepared jointly by the authors.

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The third species described in this study was collected from the Williston Limestone. This species exhibits unique morphological structures that warrant its separation into a new genus and subfamily of the Balanomorpha. An analysis of its structure indicates that this new form has a remarkable resemblance to those epizootic barnacles, occurring on whales, turtles, and other animals, that are included in the Chelonibiinae and Coronulinae (see fig. 7). Presently, there is a marked difference in temporal sequence between the stratigraphic occurrence of this extinct Eocene barnacle and the earliest records of the Coronulinae (lower Pliocene) and Chelonibiinae (lower Miocene), indicating that these two groups are significantly older than paleontological evidence heretofore indicated.

Stratigraphic relationships and faunal zonation of the Ocala sediments in peninsular Florida were the subject of a recent study by Puri (1957). More recently, Cheetham (1963) briefly discussed the regional relationships of the Ocala lithologies and biofaunal zones, in addition to presenting a discussion on the paleoecology of the Ocala Group. Puri (1957) based the biostratigraphy of the Ocala largely on ostracods and foraminifers, whereas cheilostome Ectoprocta served as the basis for the work of Cheetham (1963). Cheetham (1963) postulated that the calcareous Jackson sediments accumulated on a submarine plateau at least 200 miles long and 100 miles wide, termed the Ocala Bank, at a depth, in early Jackson time, of about 50 meters. By late Jackson time the bank had tilted so that the southern end was the more deeply submerged, the northern being significantly shallower, possibly awash.

During the Jacksonian, the Ocala Bank was decidedly tropical and was typified by a macrofauna rich in numbers of individuals but poor in numbers of species. Prior to lithification, the Williston sediments over large areas probably offered few sites for broadly attached benthonic organisms, and the shifting of these foraminiferal-rich sediments by current action no doubt contributed to limiting the development of a rich and varied fauna. Hydrographical conditions over the bank biotope during deposition of the Williston were postulated as being relatively uniform. According to Cheetham (1963), the salinity was within the limits of normality, hydrotemperatures ranged from 23° C. to 26° C., and water agitation was moderate.

ACKNOWLEDGMENTS

Special thanks are due to Mr. J. Collins of London, England, who provided specimens of *Balanus unguiformis* from the Isle of Wight. These

specimens have served as the basis of comparison with the North American forms contained in the collections of the Department of Fossil Invertebrates of the American Museum of Natural History.

SYSTEMATIC DESCRIPTIONS

ORDER THORACICA DARWIN, 1854

SUBORDER BALANOMORPHA PILSBRY, 1916

FAMILY BALANIDAE LEACH, 1817¹

SUBFAMILY BALANINAE LEACH, 1817

GENUS *KATHPALMERIA* ROSS, 1965

TYPE SPECIES: *Kathpalmeria georgiana* Ross (1965c), by original designation.

Kathpalmeria georgiana Ross, 1965

Kathpalmeria georgiana Ross, 1965c, p. 63, figs. 1, 2a-f, Barnwell Formation, Upper Eocene, Shell Bluff Landing, Burke County, Georgia.

The genus *Kathpalmeria* is characterized by solid, moderately to strongly folded parietal plates, of which the rostrum, laterals, and carinolaterals either lack or possess diminutive radii. Re-entrants of the wall plates form buttresses on the inner shell surface. Commonly, growth ridges are best preserved exteriorly in the re-entrants.

One specimen in the present collections (A.M.N.H. No. 28465) is tentatively believed to be conspecific with *K. georgiana*. The specimen in question consists of an impression of the outer shell surface of the carina, left lateral and carinolateral, and the right carinolateral. The impressions of the re-entrants show parallel, horizontal, alternating ridges and striations that represent the growth ridges of the shell.

Because the specimen is not complete, it is impossible to provide precise measurements. However, the height of the shell was probably somewhere in the range of 6 mm. to 9 mm.

OCCURRENCE: The specimen was collected in a limerock quarry about 200 yards south of the Withlacoochee River, NE. 1/4, sect. 12, T. 17 S., R. 16 E., Citrus County, Florida; Inglis Limestone, Ocala Group, Upper Eocene; collector, Arnold Ross, May, 1965.

¹ Pilsbry (1916, p. 48) acknowledged Gray as the author of the familial term Balanidae. The study by Leach, which satisfies the provisions of the International Code of Zoological Nomenclature, antedated Gray's by eight years; therefore, Leach is rightfully the author of this family (see Ross, 1966).

REMARKS: Balanidae with non-tubiferous parietal plates are generally accepted as the primitive stock from which those forms with parietal tubes arose (Darwin, 1854a, p. 172; Zullo, 1960, p. 2084). Darwin referred all those species with solid parietes to one section (=subgenus) of *Balanus*. He included a hesperibalanid (*B. unguiformis*) in this group, a species that "... presents to the systematist a most unfortunate peculiarity, in the parietes being almost as often as not permeated by small pores" (1854a, p. 297). It has been pointed out that these tubes are not developed in the same manner as those of *Balanus* (*sensu stricto*), therefore are not homologous (Kolosváry, 1956, p. 187). Yet some hesperibalanids do develop tubes and have well-developed radii, and in this regard they are more advanced than *Kathpalmeria*. In view of the fact that *Kathpalmeria*, a solid-wall form, occurs as early as the Middle Eocene (Ross, 1965c, p. 62), and ancestral balanids have been inferred to occur in Cretaceous sediments (Zullo, 1960, p. 2084); it is unlikely that the hesperibalanids are the most primitive group of the Balanidae.

Darwin (1854a, p. 122), Pilsbry (1916, p. 291), and Withers (1928, p. 44) emphasized that the Chthamalidae are a more archaic group than the Balanidae, a supposition borne out by the fossil record. In *Catophragmus*, *Pachylasma*, and *Hexelasma*, primitive chthamalids, radii are wanting, or they are extremely narrow and poorly differentiated. Noteworthy is the fact that differentiation of the carinad margin of the parietes into radii is not a fundamental feature in the Balanomorpha, since available evidence indicates that the ancestral balanid shell had solid walls without radii, as do those of the primitive Chthamalidae. In view of the foregoing, it appears reasonable to interpret *Kathpalmeria* as more primitive than the hesperibalanids.

GENUS *BALANUS* DA COSTA, 1778

SUBGENUS *HESPERIBALANUS* PILSBRY, 1916

TYPE SPECIES: *Balanus hesperius* Pilsbry (1916), Recent, Bering Sea, 56 fathoms, by original designation.

Balanus sp. aff. *B. unguiformis* Sowerby, 1846

Balanus unguiformis SOWERBY, 1846, pl. 648, fig. 1, Upper Eocene (Bartonian), Colwell Bay, Isle of Wight, type locality herein designated. ZULLO, MS, p. 21, Middle and Upper Eocene, Alabama.

Balanus sp. aff. *B. unguiformis*: WITHERS, 1953, p. 72, Upper Eocene, Mississippi.

Two specimens in the present collections (A.M.N.H. No. 28464) are provisionally considered conspecific with the hesperibalanid *B. ungui-*

formis. Both specimens are internal impressions, one of a carina, and the other of a left lateral or carinolateral compartment. Based on the impression, the sheath was approximately one-half of the height of the shell, with a moderately shallow, narrow pocket behind it. The carina, measuring 8.7 mm. in height, has poorly developed internal ribbing. The lateral compartment, measuring 5.3 mm. in height, on the other hand, shows that the internal ribbing extended to the pocket behind the sheath.

OCCURRENCE: Both specimens were collected in a limerock quarry about 200 yards south of the Withlacoochee River, NE. 1/4, sect. 12, T. 12 S., R. 16 E., Citrus County, Florida; Inglis Limestone, Ocala Group, Upper Eocene; collectors, Jackson E. Lewis and Arnold Ross, May, 1965.

REFERRED SPECIMENS: A.M.N.H. No. 28463; *Balanus unguiformis* Sowerby, 1846; Middle Headon Beds ("Venus Bed"), Lower Oligocene (Lattorfian); Whitecliffe Bay, Isle of Wight; collector, J. Collins. A.M.N.H. Nos. 10333a/1 and 10333b/1; *Balanus* sp. aff. *B. unguiformis* Sowerby, 1846; "Eocene Claiborne Sands; Claiborne, Alabama; Hall Collection"; original label identifies specimens as *Balanus finchi* Lea. A.M.N.H. Nos. 10333c/1 and 10333d/1; *Balanus* sp. aff. *B. unguiformis* Sowerby, 1846; "Eocene Claiborne Beds; Claiborne, Alabama; Hall Collection"; original label identifies specimens as *Balanus finchi* Lea. A.M.N.H. No. 24866a; *Balanus* sp. aff. *B. unguiformis* Sowerby, 1846; Gosport Sand, Middle Eocene, Claiborne Group, Claiborne Landing, Alabama; collectors, Donald F. Squires and William Heaslip, August, 1955. A.M.N.H. No. 24866b; *Balanus* sp.; Gosport Sand, Middle Eocene, Claiborne Group, Claiborne Landing, Alabama; collectors, Donald F. Squires and William Heaslip, August, 1955.

REMARKS: The specimens from the Isle of Wight agree closely with the description of *B. unguiformis* presented by Darwin (1854a, p. 296). However, none of them can be referred to the ribbed form *erisma* Sowerby (1846), for which, like *B. unguiformis*, Sowerby provided neither description nor locality data. In general, the shell of *B. unguiformis* is low-conic, and the parietes are relatively smooth. The radii are well developed and abut against the adjoining compartment. Internally, the surface is ribbed, and the ribs commonly extend upward into the narrow and shallow pocket behind the sheath. The sheath covers the upper one-half or less of the inner wall. About one-half of the specimens examined have parietal tubes that extend to the apex of the wall plate. These tubes are not considered homologous with those found in *Balanus* (*sensu stricto*), as noted above.

A large number of specimens in the Hall Collection (A.M.N.H. Nos.

10333a/1 and 10333c/1), from Middle Eocene sediments in Alabama, are hesperibalanids in the strict sense. These specimens exhibit few, if any, differences from the solid-wall forms of the Lattorfian Middle Headon Beds, and they are therefore tentatively referred to *B. unguiformis* until such time as the opercular valves become available for study.

The specimens indicated as lots Nos. 10333b/1 and 10333d/1 in the Hall Collections differ from the foregoing specimens in that parietal tubes, and therefore an inner lamina, are present. Furthermore, the tubes appear to represent an early stage in the development of parietal tubes of the *Balanus* (*sensu stricto*) type. They are rectangular and extremely short, hardly more than 1 mm. in a shell approximately 5 mm. in height. The basal edges of the longitudinal septa separating them, although worn, appear to have been crenated. The inner surface of the outer lamina bears longitudinal septa that do not extend to the inner lamina.

The fourth lot of specimens in the American Museum Fossil Invertebrate collections referable to *B. unguiformis* are from the Gosport Sand. The 20 or so specimens (A.M.N.H. No. 24866a), with one exception noted below, have somewhat larger and thicker shells than specimens from the Hall and Middle Headon Beds collections. Moreover, the teeth of the sutural surface of the radii tend to be bifid or trifid rather than arranged as a simple horizontal bar. Whether these differences are within the range of variability of the species or are of systematic value is presently unknown.

Darwin (1854b, p. 26) described and figured a specimen from the Upper Pliocene (Plaisancian) Coralline Crag of England which he named *Balanus bisulcatus* var. *plicatus*.¹ A specimen from Suffolk, England, was recently assigned to *plicatus* by Davadie (1963, pl. 41, fig. 3). The variety *plicatus* was characterized as having deeply folded walls and narrow radii with oblique summits. The parietal plates of the nominate variety are non-tubiferous. Unfortunately, Darwin made no reference to the condition of the wall plates in the variety *plicatus*.

One specimen in the present collections from the Gosport Sand, al-

¹ As a synonym of his species *B. bisulcatus*, Darwin listed *B. sulcatus* Nyst, stating "I am indebted to M. Bosquet for a specimen, bearing this name and reference, found in the 'Système Bolderien' of Dumont (miocene according to Sir C. Lyell) at Bolderberg. The specimen consists of a rostrum, with a portion of the base attached; and as these parts are in some degree characteristic, I fully believe this specimen to be the *B. bisulcatus*" (Darwin, 1854a, p. 293, footnote). *Balanus sulcatus*, then, is a senior synonym of *B. bisulcatus*, and it must be considered a *nomen oblitum* according to Article 23 (b) of the International Code of Zoological Nomenclature.

though much larger than the specimens described by Darwin (1854b) and figured by Davadie (1963), has an external appearance similar to the variety *plicatus*. The specimen in question is a strongly ribbed rostral plate, the ribs being acute, high, three in number, and equidistantly spaced. The central rib is higher and more prominent than the lateral ones. The sutural edges of the radii, although worn, appear to have had teeth with subsidiary basal denticles. Development of the sheath and the internal ribs is similar to that found in *B. unguiformis*. One significant difference is the development of parietal tubes that extend from the apex to the base of the plate in much the same manner as in the tubiferous balanids. Basally, the tube openings are rectangular in section, and incomplete septa are present on the inner face of the outer lamina. That the Gosport and Coralline Crag forms are conspecific is unlikely, but the opercular valves must be found before more definite conclusions can be reached. Moreover, it should be noted that this specimen cannot be referred to *Hesperibalanus* in view of the development of parietal tubes of the *Balanus* (*Balanus*) type.

EMERSONINAE ROSS, NEW SUBFAMILY

DEFINITION: Included in this subfamily are those Balanomorpha with numerous, parallel rows of rectangular to square, septate parietal tubes. This unique construction results from the development of intercalated laminae.¹

EMERSONIUS ROSS, NEW GENUS

DEFINITION: This genus is defined as having a large, low, conic, balanoid shell, which is inferred as having six wall plates (rostrum with radii, laterals, carinolaterals, and carina). The parietes and radii are tubiferous, with transverse septa uniformly distributed throughout each tube. Intercalated laminae occur between the inner and outer laminae and extend from the apex to the base. Distinct, arborescent teeth are developed on the articulating surface of the radii. The basis is probably membranous. *Emersonius cybosyrinx*, new species, is here designated as type species of this genus.

ETYMOLOGY: This new genus is named in honor of Dr. William K. Emerson, Chairman of the Department of Living Invertebrates, the American Museum of Natural History.

¹ Intercalated laminae, known in no other balanomorph, are herein defined as lamina that originate from the outer lamina and lie parallel to, and in the same plane as, the inner lamina.

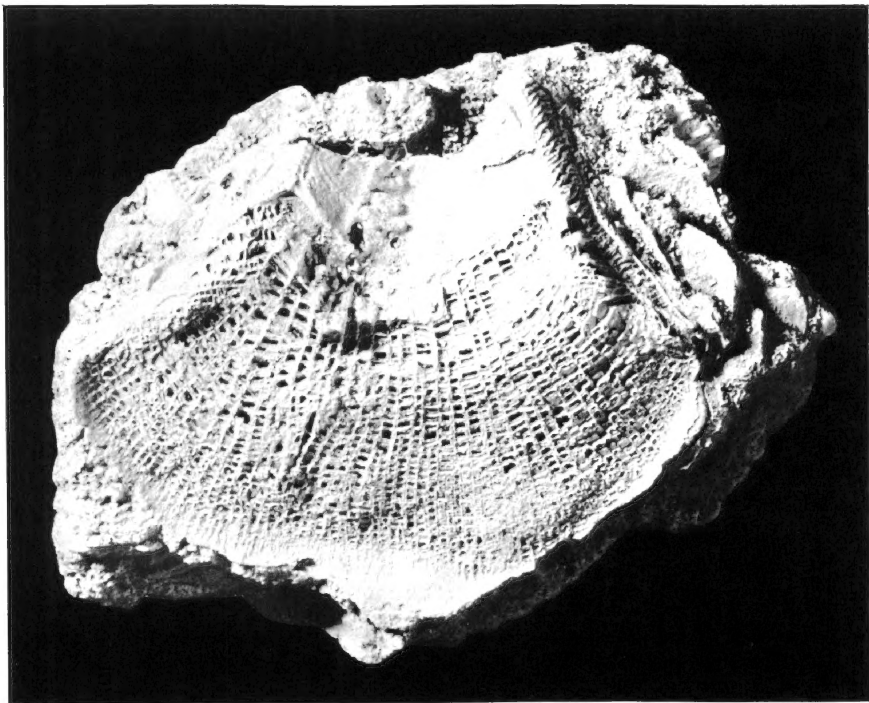


FIG. 1. *Emersonius cybosyrinx* Ross, new genus and species; Williston Limestone, Upper Eocene, Florida; holotype, A.M.N.H. No. 28462; view of internal surface of rostrum. The base, bounded by the inner and outer laminae, is crossed by longitudinal and intercalated septa, resulting in a honeycombed appearance. It can be observed that the inner lamina is continuous with the sheath, in which the alar depression of the right lateral compartment is visible. The sutural surfaces of the radii are also visible. Actual width of specimen, 30.8 mm.

Emersonius cybosyrinx Ross, new species

DIAGNOSIS: Since there is but a single species known, the diagnosis is the same as that for the genus.

DESCRIPTION: The description that follows is based on a rostral plate only.¹ The plate is low and relatively thick; therefore the shell was low-conic. External ornamentation is probably limited to fine growth lines. After the encrusting matrix had been removed, there was no indication

¹ During preparatory work on this specimen, the senior author recognized that plaster-of-paris duplicates would be of value to other workers. A large number of these have been prepared, and they are available on request from the senior author.

of very fine growth ridges, possibly owing either to post-depositional alteration or to the cleaning process. Less than one-half of the inner wall is covered by a sheath, the basal margin of which does not depend freely. The face of the inner lamina, where preserved, appears to be systematically and uniformly ribbed, the ribs being equidistantly spaced, very low, and narrow (fig. 1). These ribs appear to have extended to the sheath. The parietal tubes range from rectangular to square in cross section, and proceed in a decreasing series of sizes from the inner to the outer lamina (figs. 1 and 6C). These tubes extend from the base to the apex of the plate, and transverse septa occur throughout their length at regular close-spaced intervals (fig. 6C).

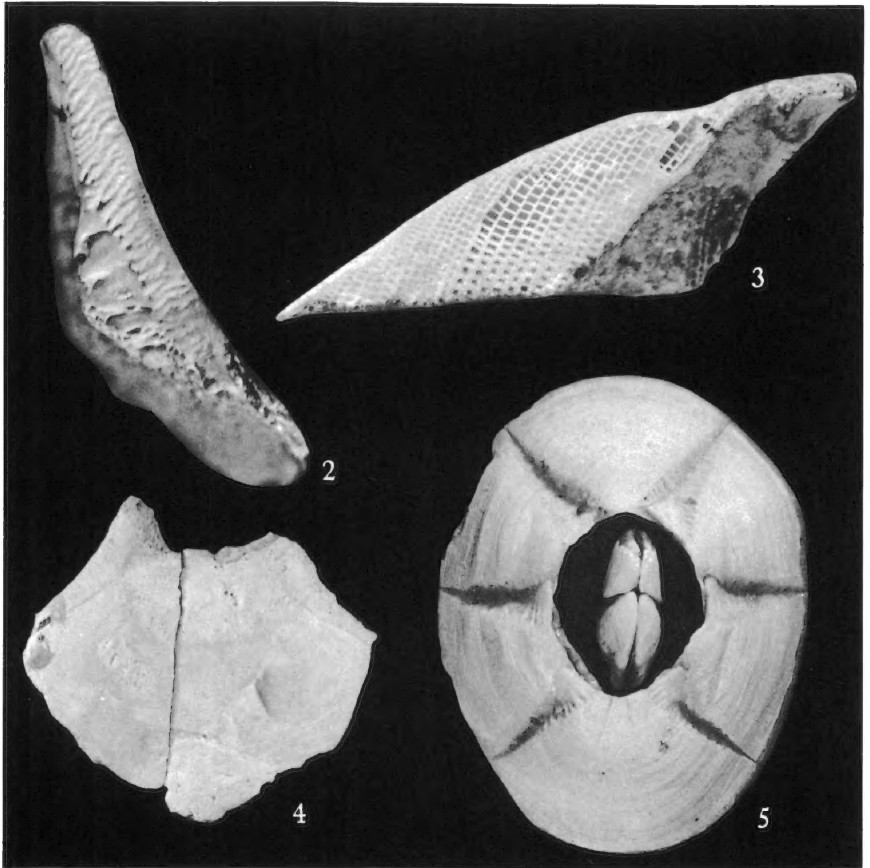
The nature of the basis is a matter of deduction. The basal edges of the longitudinal septa are devoid of teeth that would serve as an interlocking mechanism with similar intercalating structures of a calcareous basis. Their absence implies that the basis was membranous. Furthermore, the extremely broad surface that comes in contact with the substratum is the type of attachment found in Recent forms with a membranous basis, e.g., *Chelonibia*, *Tetracrita* (*sensu lato*), and *Balanus cariosus*.

The lateral margins of the rostrum are differentiated into distinct radii. The outer surfaces of the radii are slightly lower than the surface of the paries (fig. 4). The articular surfaces of the radii are ridged with arborescent teeth (fig. 2). The radii are permeated by parallel rows of transverse septate tubes, similar to the vertical rows of the paries (fig. 4).

MEASUREMENTS OF HOLOTYPE: Owing to the fact that there is only one partially eroded compartment, no precise measurements can be given. One dimension, the maximum width of the compartment, was determined to be 30.5 mm. In a normal growth position, the height of the shell was probably about 8.5 mm. An estimate of the rostracarinal diameter, based on the reconstruction and comparison with *Chelonibia testudinaria*, is in the range of 55 mm. to 60 mm.

TYPE LOCALITY AND HORIZON: The specimen was collected in an abandoned limerock quarry about 0.5 mile north of Florida Highway 26, and approximately 3.3 miles west of the United States Interstate Highway 75 overpass, NW. 1/4, sect. 35, T. 9 S., R. 18 E., Alachua County, Florida (latitude 29° 30' N., longitude 82° 30' W., approximately); Williston Limestone, Ocala Group, Upper Eocene; collector, Arnold Ross, March, 1964.

TYPE DEPOSITORY: The sole specimen (No. 28462) is deposited in the collections of the Department of Fossil Invertebrates of the American Museum of Natural History.



FIGS. 2-4. *Emersonius cybosyrinx* Ross, new genus and species; Williston Limestone, Upper Eocene, Florida; holotype, A.M.N.H. No. 28462. 2. Articulating surface of left radius, in lateral view, showing arborescent teeth. $\times 3$. 3. Cross-sectional view of shell where broken along primary septum; transverse septa, intercalated laminae, and inner and outer laminae visible. $\times 3$. 4. External surface of rostral plate, showing radii slightly below surface of parietes and the exposed transverse septa in the tubes of the right radius. The break in the shell existed in the fossil when found and provided the cross section which is illustrated in figure 3. $\times 1.5$.

FIG. 5. *Chelonibia testudinaria* (Linnaeus), 1758, from carapace of *Eretmochelys imbricata squamata*, Magdalena Bay, Baja California, Mexico. Note facies similarity between rostrum of this species and *E. cybosyrinx*. $\times 1.1$.

ETYMOLOGY: The specific name is derived from Greek *kybos* (cube) and *syrinx* (tube) and denotes the fact that the species is characterized by parietal tubes with boxlike chambers.

REMARKS: The number of parietal plates is inferred to be six. This inference rests on the fact that the rostrum, having radii, is compound. Therefore, the number of parietal plates could not have been eight.

Emersonius outwardly has many features in common with the Tetraclitinae, among which are the large number of parietal tubes, the membranous basis, a sheath that is not free from the inner lamina, and arborescent teeth on the sutural edges of the radii. At the present state of our knowledge, it can only be assumed that these features were independently derived in the Tetraclitinae. Three structures that serve to separate *Emersonius* from the Tetraclitinae are the six wall plates, transverse parietal septa, and the fact that the square or rectangular parietal tubes occur in parallel rows. Of the presently known Balaninae, only a few of the coral-inhabiting pyrgomatids and *Balanus cariosus* have several rows of parietal tubes, but these are circular or oval in section, relatively few in number, not provided with transverse septa, and they are not formed by intercalated laminae. Consequently, nothing suggests close affinities of *Emersonius* with these groups.

The balanomorphs that bear close resemblance to *Emersonius* are the chelonibiines and coronulines. In the general form of the shell (rostrum), the broad basal margin of the parietes, and membranous basis *Emersonius* clearly approaches *Chelonibia*.

Although the rostralaterals are partially concrescent with the rostrum in *Chelonibia*, the sites of concrescence are clearly visible internally, and partially visible externally, especially near the apex (see fig. 5). Therefore, the rostrum in *Chelonibia* is composite and has radii, rather than being simple and provided with alae, as in more primitive eight-plated forms. Although the rostral plate of *Emersonius* shows no such sites of concrescence, it has radii and must be a composite plate. A comparison of the rostrum of *Emersonius* with a rostrum of comparable size from *Chelonibia* (figs. 4 and 5) shows that the two plates have essentially the same proportions, provided the assumption that the shell of *Emersonius* was oval in basal outline as it is in *Chelonibia* is correct. Attempts to find a "best fit" for a reconstruction of *Emersonius* indicates that only five additional plates, arranged as in *Chelonibia*, are necessary (paired laterals and carinolaterals, and a carina). Although it is possible that the carinolaterals were concrescent with the carina or the laterals, there is no evidence to suggest that such would have been the case.

However, several distinct differences between *Chelonibia* and *Emersonius* should be mentioned, specifically the bilamellar radii, numerous septate parietal tubes, as well as only six parietal plates. Furthermore, in *Chelonibia* the sheath is separate from the inner lamina and forms a significant

portion of the inner wall, whereas in *Emersonius* it does not. There are a number of similarities between *Emersonius* and the coronulids, in particular, the parietal tubes in *Platylepas* and *Tubicinella*, which, although in but a single row, are composed of similar boxlike chambers. In addition, *Platylepas* develops a bilamellar radius, and has an adpressed sheath, as does *Tubicinella*. These detailed similarities indicate a close relationship between *Emersonius* and these groups of barnacles.

Emersonius combines characters of both complexes within this group of epizootic barnacles; therefore it cannot be assigned to either the Chelonibiinae or the Coronulinae. Furthermore, *Emersonius* contains a unique skeletal structure, intercalated laminae. In consideration of these complexities, it is necessary to place *Emersonius* in a subfamily of its own.

ONTOGENY AND PHYLOGENY OF *EMERSONIUS*

The balanomorph shell is unique among exoskeletons of extant marine crustaceans. The uniqueness lies in the fact that the shell is not molted and therefore contains within its structure a record of its ontogenetic development. Furthermore, it has attained a degree of complexity that is unparalleled among the Crustacea. Owing to the calcitic nature of the barnacle shell, it is often readily fossilized in its original state. Consequently, many ontogenetic details are frequently retained that aid in the unraveling of the phylogeny of the group that it represents.

Emersonius cybosyrinx, from the Eocene of Florida, represents an organizational plan that is unparalleled in the presently recognized fossil and extant Balanomorpha.

Although there is but a single wall plate of *Emersonius cybosyrinx* it is possible to trace much of the ontogeny of the shell to its present form. The exoskeleton of this species, and its mode of development, are more complex than anything thus far encountered in the Balanomorpha. Interesting is the fact that shell development in this form combines features common to the turtle-barnacles *Platylepas* and *Chelonibia*, features that allow one to draw inferences on its affinities with this complex of the Balanidae.

ONTOGENY

The wall, as observed, consists of inner and outer laminae diverging from the apex. Additionally, there are four major, internal, structural elements (see fig. 6C and F): (1) primary septa passing from the inner to the outer lamina; (2) secondary, tertiary, and quaternary septa, intercalated between the primaries, extending in echelon, from the outer

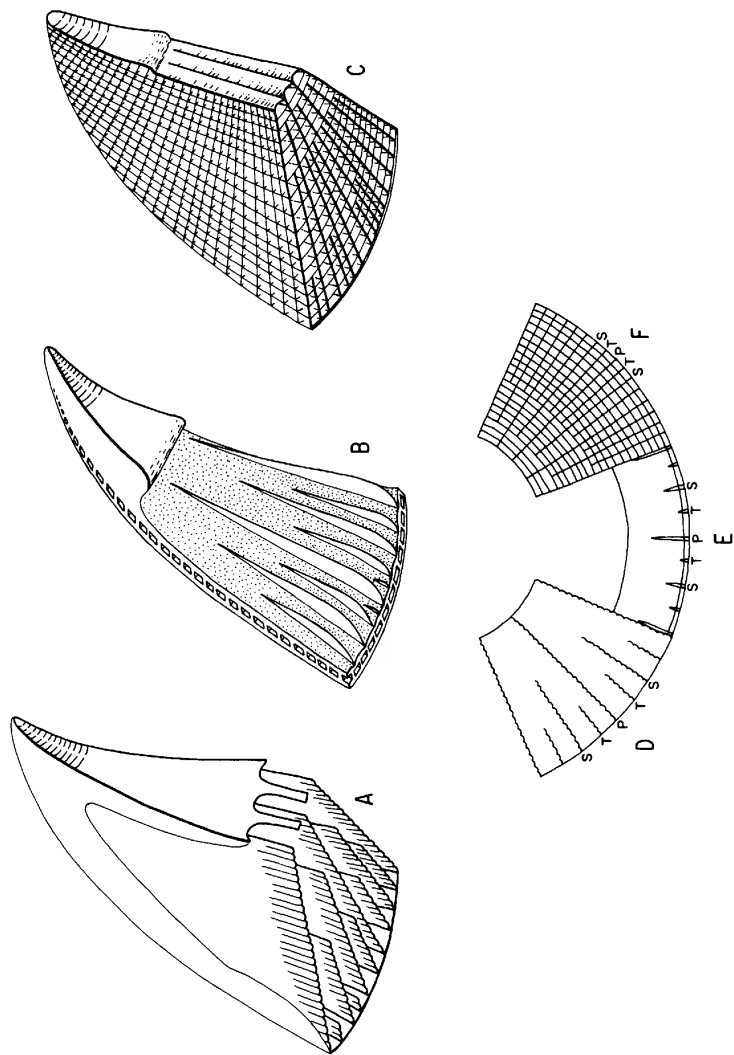


FIG. 6. Schematic projection of portions of walls. A. *Chelonibia*. B. *Platylepas*. C. *Emersonius*. D-F. Corresponding plan views of the same. Abbreviations: P, primary septum; S, secondary septum; T, tertiary septum.

lamina inward, but not reaching the inner lamina; (3) intercalated laminae, lying in the same plane as the inner lamina, arrayed in a closely spaced series, each extending downward from the outer lamina to the base; and (4) transverse septa, lying normal to the inner lamina and intercalated laminae, and forming a close-spaced laminar series extending from the apex to the base.

In studying the structural details of the wall of *E. cybositynx*, one can separate a number of significant ontogenetic steps in its development. That the wall plate is initially solid, as it is in all other Balanomorpha, cannot be actually observed, but it may be inferred. Whether the wall tubes develop basally in forming inner and outer laminae and primary longitudinal septa [as is no doubt the case in the primitive balanomorphs *Platylepas*, *Tetraclita* (*Tesseropora*), *Balanus cariosus*, and *B. balanoides*; see Gutmann, 1960], or whether longitudinal septa appear on the inner surface of the outer lamina, and the inner lamina is developed secondarily between the distal ends of the longitudinal septa (as in *Balanus, sensu stricto*), cannot be determined (see Costlow, 1956; Newman, Zullo, Wainwright, in press). The former method is known to occur in those forms with a membranous basis, and the latter, in those forms with a calcareous basis. Available evidence indicates that the former, whereby the wall perforates basally, is the method employed by *Emersonius*.

Beginning with a solid wall in *Emersonius*, the tubular nature of the shell would have been initiated by a marginal growth process that results in a wall with a perforated appearance, i.e., tubes separated by primary longitudinal septa. Growth along the perforated basal margin proceeds for a short period before the tissue contained within the tubular perforations is withdrawn a short distance and a transverse septum deposited. This process is then repeated several times, resulting in a wall composed of a single series of boxlike chambers, each generation lying in exactly the same plane. Such a serial repetition of the chambers is seen in no other balanomorph, except *Platylepas*.

It has not been possible to determine how long this single series of chambers continues to develop, but by the time the wall is 1 mm. to 2 mm. high, the first intercalated lamina appears. This lamina develops by perforation of the outer lamina, in exactly the same manner as the initial wall perforation that resulted in the development of the inner and outer laminae. Continued growth now leads to the enlargement and deepening of both series of boxlike tubes. Periodically the tissue within the new series of developing tubes withdraws, just as it did and continues to do in the first series, and new transverse septa are laid down. At this stage of development the wall is composed of two parallel series

of chambers. No sooner have a few chambers in the second series been formed, than the basal margin of the outer lamina again perforates, resulting in a wall, three series of chambers thick. This process is repeated until there are some 30 intercalated laminae, with serially arrayed chambers lying between them.

In the discussion presented thus far, we have been concerned with the development of intercalated laminae and transverse septa of the wall, as seen along the plane of a primary longitudinal septum (fig. 6C). The discussion that follows is concerned with the growth of secondary, tertiary, and quaternary longitudinal septa that add further to the complex nature of the wall (see fig. 6F).

In viewing the basal margin of the shell, one can determine that the innermost two or three series of chambers occupy completely the space between the primary longitudinal septa. At the initiation of the next intercalated lamina two chambers appear, whereas the preceding area had been occupied by one. This process is concomitant with the development of a secondary longitudinal septum. Further growth results in several series of chambers within the confines of this pattern before the tertiary longitudinal septa are intercalated in exactly the same manner, i.e., two chambers appear, whereas the preceding area had been occupied by one. The quaternary, quinary, and so on, longitudinal septa follow thereafter, effectively in regular succession.

This type of complex wall has been found in no other member of the Balanomorphs, yet it did not evolve *de novo* but must have developed from a simpler design. Among the turtle-barnacles a basically similar plan is observed. This can be seen by comparing figure 6A, B, and C. The more simply designed wall of *C. testudinaria* has the basic elements in the serial arrangement of longitudinal septa (fig. 6D). On the other hand, the simple chambered wall of *Platylepas* has the basic elements for the formation of a serially arrayed, multichambered wall (fig. 6E). A combination of these features results in the development of the type of wall found in *Emersonius*.

PHYLOGENY

The foregoing analysis of the ontogeny of the shell is based on the available factual evidence. On the other hand, there is a pronounced facies similarity between certain epizootic barnacles, such as those found on turtles or comparable life forms (e.g., xiphosurans, large decapod crustaceans, and others; see fig. 7) and *Emersonius*. But that *E. cybosyrinx* was epizootic can only be assumed.

If it were for this facies similarity alone (e.g., low conic form, large

size, exceptionally broad base of attachment, and biofacies in which it was found), one would be hesitant to place great weight on the suggested habitus. However, it has been shown that many of the details in the structure of *Emersonius* find their counterparts in the extant turtle-barnacles. These are the membranous basis, tubes in the radii, in echelon series of longitudinal septa, and the initial development of serially sealed, boxlike chambers of the wall. By these structural similarities we are again compelled to look to the turtle-barnacles in an attempt to deduce the affinities of *Emersonius*. Furthermore, as is mentioned above, the nature of the substrate in the habitat where the barnacle was found appears to preclude its having settled and grown on an inanimate object.

The most generalized members of this group of epizootic barnacles are *Platylepas* and *Chelonibia patula*. The development of buttresses in *Platylepas* is a specialization of no fundamental importance as far as the Balanomorpha are concerned, having the same functional significance as the broadly based, longitudinal septa in *Chelonibia*, i.e., adding vertical support to a comparatively peltate form. By reduction in the extent of the longitudinal septa, *Chelonibia* would approximate closely the basic form of *Platylepas*. By elimination of the buttresses, *Platylepas* assumes the grade of organization from which both of these forms were no doubt derived. In that *Chelonibia* has a true rostrum and therefore has the fundamental number of plates, eight rather than six as seen in *Platylepas*, it seems probable that the stem complex itself must have been eight-plated.

An important feature that separates *Platylepas* from *Chelonibia* is the row of serially arranged, boxlike chambers present in the wall of the former. That the stem line had, as a group, a wall permeated by boxlike chambers is possible but cannot be demonstrated. However, present evidence suggests that that segment of the stem complex giving rise to *Platylepas*, although closely related to the chelonibiids, had a platylepadine wall (e.g., serial repetition of boxlike chambers). Given these relationships, *Emersonius*, although sharing similarities with *Platylepas* and *Chelonibia*, would have had its origins closer to the platylepadine than to either the chelonibiid or coronuline line.

In the Paleogene the Balanomorpha were undergoing a period of explosive evolution, a time during which certain groups undoubtedly became specialized to an epizootic habitus. Germane to the present discussion are those forms (chelonibiids and platylepadines) that became adapted to living on vagile organisms, such as large marine arthropods, reptiles, and mammals. The most generalized surviving members of these two groups of barnacles (*Chelonibia patula* and *Platylepas*) inhabit the

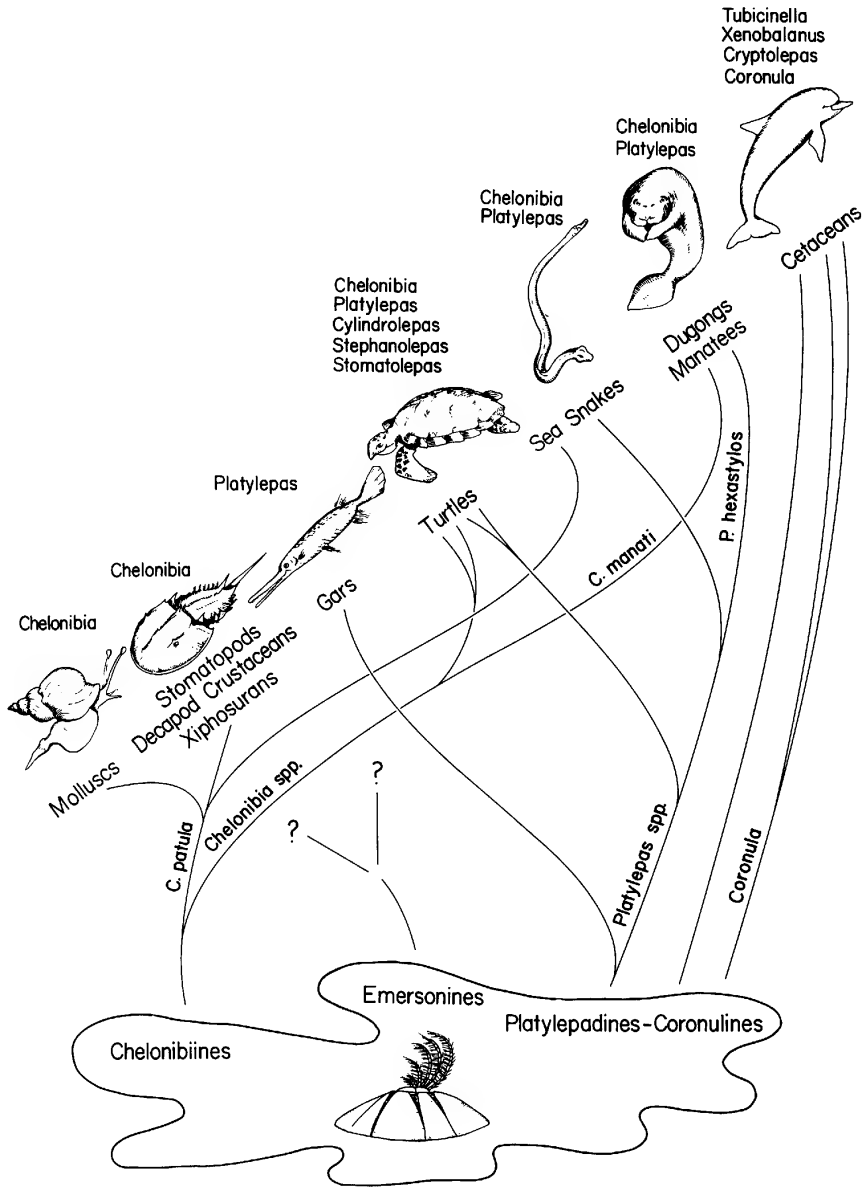


FIG. 7. Distribution of chelonibiid and coronulid genera with regard to host, the hosts arranged in approximate order of their appearance in the sea. Note diversity of hosts occupied by generalized forms *Chelonibia* and *Platylepas*, the former in the main having exploited higher invertebrates and marine reptiles, and the latter, marine reptiles and mammals. The early occurrence, large size, and structural complexity in *Emersonius* suggest a high degree of host specificity within the mollusk-turtle segment of the available host types.

broadest spectrum of host forms, whereas the more specialized types are relatively restricted in their host requirements (see fig. 7). The new genus described herein is a highly specialized form. It follows then that its adaptation was in relationship to a particular host. This host could have been a turtle-like form, or even a nautiloid such as *Aturia*, or a crab such as the xanthid *Ocalina*; forms of the latter two occur at the same horizon (Lewis and Ross, 1965). Indeed, it seems likely that the demise of *Emersonius* was the extinction of its host.

FOSSIL CIRRIPIEDIA OF FLORIDA

In the following chronological list, all the Tertiary and Pleistocene barnacles reported from Florida are cited by formational occurrence. Those species reported here for the first time are preceded by an asterisk; previously recorded species are followed by references to the literature.

MIOCENE

Tampa Limestone

Balanus humilis Conrad, 1846 (Conrad, 1846, p. 400; Ross, 1965c, p. 59)

Hawthorne Formation

**Balanus humilis* Conrad, 1846

Choctawhatchee Formation

Scalpellum gibbum Pilsbry, 1916 (Ross, 1965d, p. 219)

Balanus talquinensis Weisbord, 1966 (Weisbord, 1966, p. 37)

Balanus leonensis Weisbord, 1966 (Weisbord, 1966, p. 43)

Balanus ochlockoneensis Weisbord, 1966 (Weisbord, 1966, p. 46)

Balanus bloxhamensis Weisbord, 1966 (Weisbord, 1966, p. 48)

**Balanus* sp. aff. *B. improvisus* Darwin, 1854

Balanus sp. (DuBar and Beardsley, 1961, p. 170)

Tamiami Formation

Balanus trigonus Darwin, 1854 (Ross, 1965a, p. 271)

Balanus glyptopoma Pilsbry, 1916 (Pilsbry, 1916, p. 102; Ross, 1965a, p. 271)

Balanus concavus Bronn, 1831 (MacNeil in Parker *et al.*, 1955, p. 87; DuBar, 1962, p. 17)

Balanus concavus proteus Conrad, 1834 (Ross, 1964, p. 488; Ross, 1965a, p. 271)

Balanus tamiamiensis Ross, 1965 (Ross, 1965a, p. 272)

Balanus tintinnabulum (Linnaeus), 1758 (Cornwall, 1962, p. 624)

Balanus sp. (DuBar, 1958, p. 216; DuBar, 1962, p. 59)

Chelonibia testudinaria (Linnaeus), 1758 (Ross, 1963c, p. 227; Ross, 1965a, p. 271)

Chelonibia patula (Ranzani), 1818 (Ross, 1963c, p. 225; Ross, 1965a, p. 271)

Burrows of an acrothoracican (Ross, 1965e, the genera *Lithoglyptes* and *Kochlorine* are known to occur in the Caribbean, p. 317)

PLIOCENE

Caloosahatchee Formation

**Balanus niveus* Darwin, 1854

Balanus sp. (DuBar, 1958, p. 221; DuBar, 1962, p. 81)

- Pyrgoma prefloridanum* Brooks and Ross, 1960 (Brooks and Ross, 1960, p. 355)
Chelonibia testudinaria (Linnaeus), 1758 (Ross, 1963c, p. 227)
Chelonibia sp. (Ross, 1963c, p. 230)

PLEISTOCENE

Fort Thompson Formation

- Balanus* sp. (Parker *et al.*, 1955, p. 95; DuBar, 1962, p. 81)
Pyrgoma sp. (Parker *et al.*, 1955, p. 95)

Anastasia Formation

- **Balanus* sp. aff. *B. niveus* Darwin, 1854

Pamlico Formation

- Balanus niveus* Darwin, 1854 (Ross, 1963b, p. 156)
Balanus sp. (Ross, 1963a, p. 229)
Platylepas wilsoni Ross, 1963 (Ross, 1963a, p. 229, as *Platylepas* sp.; Ross, 1963b, p. 153; Ross, 1965b, p. 278)
Chelonibia testudinaria (Linnaeus), 1758 (Ross, 1963a, p. 229; Ross, 1963b, p. 156; Ross, 1963c, p. 227)
Chelonibia testudinaria var. cf. *C. testudinaria* var. *solida* Withers, 1929 (Ross, 1963c, p. 230)

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